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## Plasticity in a changing world: Behavioural responses to human perturbations

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8 Title: Plasticity in a changing world: Behavioural responses to human perturbations

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Abstract

Most insect species are affected by Human Induced Rapid Environmental Changes (HIREC). Multiple responses to HIREC are observed in insects, such as modifications of their morphology, physiology, behavioural strategies or phenology. Most of the responses involve phenotypic plasticity rather than genetic evolution. Here, we review the involvement of behavioural plasticity in foraging, reproduction, habitat choice and dispersal; and how behavioural plasticity modifies social behavior and inter-specific interactions. Although important, behavioural plasticity is rarely sufficient to cope with HIREC. An increasing number of studies find species to respond maladaptively or insufficiently to various anthropogenic disturbances, and less often is large degree of plasticity linked to success.

## 53 Introduction

54 Most insect species are affected by Human Induced Rapid Environmental Changes (HIREC, defined by Sih et al. 2011)[1],  
55 which include variable threats like climate change, habitat fragmentation, habitat loss, human harvesting, and pollution.  
56 The species can respond to HIREC, as to any other environmental changes, through plasticity, genetic evolution or  
57 dispersal. HIREC generally impact negatively the species. However some species cope well with HIREC and their  
58 populations increase to a point where they become themselves a threat to other species. Multiple responses to HIREC  
59 are observed in insects, such as modifications of their morphology (eg, size, wing area), physiology (eg, immune  
60 response, metabolic rate), behavioural strategies or phenology [2]. Hendry et al. (2008) [3] used meta-analysis dedicated  
61 to animals and found most of the responses to involve phenotypic plasticity rather than genetic evolution. Moreover,  
62 when genetic changes or shifts in demography, distribution or phenology occurred, these were generally preceded by  
63 a modification involving phenotypic plasticity [4]. Thus, behavioural plasticity appears important in explaining variation  
64 in the success of species to resist HIREC [5] (Figure 1). The behavioural responses can be either maladaptive, such as the  
65 incapacity to detect new predators that can precede species' decline [5], or be adaptive and improve fitness, such as  
66 the finding of new host plant species by *Drosophila suzukii* when invading new areas [6]. In this chapter, we examine  
67 how behavioural plasticity is involved in insect responses to HIREC during foraging, reproduction, habitat choice and  
68 dispersal; and how behavioural plasticity modifies social behavior and inter-specific interactions. We also examine if this  
69 plasticity is sufficient to respond adaptively to HIREC or not.

## 70 Foraging behavior

71 The Optimal Foraging Theory (OFT) predicts that generalist species should turn to specialist strategies when resources  
72 become rare, such as after habitat changes due to HIREC. Species that show plasticity in their temporal or spatial  
73 resource use, such as aphid parasitoids [7], may have a higher ability to resist HIREC. The main plastic response of  
74 foraging insects to changes in their habitats is to modify or enlarge their diet choice. Evans & Moustakas (2017) [8]  
75 showed with a model that if predators (or species at high trophic level), shift among prey species when the preferred  
76 prey becomes unavailable because of climate change, they survive longer. This modification of diet has been observed  
77 in phytophagous insects, and sometimes improves resistance to climate change, as shown by Raffa et al. (2016) [9] for  
78 bark beetles, and sometimes not, as shown by Pol et al. (2017) [10] for ants. In some species, like the invasive *Drosophila*  
79 *suzukii* that shows extreme plasticity in diet choice, including more than 30 plant species, diet breadth is probably  
80 responsible for their success [6]. The capacity of this species to use transgenerational medication (preference of

81 oviposition in fruit containing an entomotoxic substance) contribute to its success [11]. However, *D. suzukii* also  
82 oviposits on plants that prevent the development of their larvae. Such traps could represent a cost of extreme plasticity  
83 [6].

84 Another solution to climatic stress is to selectively feed on particular types of food. The tropical butterfly *Bicyclus*  
85 *anyana*, decreases its activity on hot days and increases its intake of polyphenols (antioxidant) in order to maintain  
86 elevated antioxidant levels, which may confer fitness benefits by up-regulating endogenous antioxidant defenses. In  
87 grasshoppers, individuals shift their nutrient intake between carbohydrates and proteins depending on temperature  
88 and predation stress: indeed, it was shown that a chronic risk of predation (i.e. a chronic stress), induces an elevated  
89 metabolism and then a change in nutrient demand and resource consumption and that a higher temperature stands to  
90 exacerbate this stress and this diet modification. Growth or reproduction are protein-demanding whereas to cope with  
91 stress, a diet balanced towards carbohydrates is more appropriate [12].

## 92 Reproductive behaviour

93 Changes in the environment can influence the ability of individuals to attract and locate mates, as well as their mate  
94 choice behaviour. Such changes can alter the number and quality of offspring produced, as well as lead to a demographic  
95 Allee effect, and, hence, influence population dynamics [13]. Traffic noise, for instance, interferes with the ability of  
96 female field crickets *Gryllus bimaculatus* to locate singing males during mate searching, which can influence their  
97 reproductive success [14]. To counteract negative effects of noise on mate location, individuals may alter their mate  
98 attraction or mate location behaviour. For example, male grasshoppers *Chortippus biguttulus* elevate the frequency of  
99 their courtship song so that it can be distinguished from traffic noise [15].

100 Another common environmental change influencing reproductive behaviours is the increased use of artificial light at  
101 night. Male glow-worms *Lampyris noctiluca*, for instance, are less able to locate glowing females under artificial light  
102 [16], while females of the Australian black field cricket *Teleogryllus commodus* become less selective in their mate choice  
103 [17]. Increased light levels influence also sex pheromone production. For example, females of a noctuid moth *Mamestra*  
104 *brassica* reduce their sex pheromone production when light levels are high [18].

105 Changes in habitat structure are common causes of altered reproductive behaviour. An example is the degradation of  
106 tropical cloud forests, which has caused an Afrotropical butterfly *Salamis parhassus* to shift its mate search behaviour

107 from perching to patrolling [19]. Rising temperature and climate change influence in turn the production and reception  
108 of sex pheromones [20], as well as the choice of oviposition site [21].

#### 109 Choice of micro-habitat

110 The choice of micro-habitat in response to habitat and climate change has received much attention. For example,  
111 Burdick et al. (2015) [22] showed that aphids modify their feeding location under increased UV radiation by feeding on  
112 the underside of leaves, as this protects against radiation. Alford et al. (2017) [23] showed that aphid parasitoids  
113 increase their thermal tolerance and, hence, resistance to climate stress by manipulating the settling place on  
114 parasitized aphids.

#### 115 Activity

116 As mentioned previously, Beaulieu et al. (2015) [24] recorded a decrease in daily activity of the tropical butterfly on hot  
117 days. Physical activity elevates metabolic rate and the production of reactive oxygen species (ROS) and reduced activity  
118 consequently limits these effects. The ant *Iridomyrmex purpureus* (Formicidae) employs a range of strategies to  
119 overcome high temperature stress, such as adjusting time of foraging to the colder hours of the day, climbing grass  
120 blades to cool down, and foraging only within shaded areas [25].

121 The reaction to thermal stress varies among species. For example, Kruse et al. (2008) [26] showed that spiders increase  
122 their activity at high temperatures, whereas carabid beetles decrease their activity. Since both are predators on the  
123 same prey (flies), these opposite reactions modify the predation rate on the prey.

124 At the seasonal level, Tougeron et al. (2017) [27] observed a change in overwintering strategy following winter warming  
125 in aphid parasitoid wasps, from diapause to active state. This plasticity allows individuals to increase their progeny  
126 production. The mechanism behind the change is a decrease in responsiveness to environmental signals, rather than a  
127 genetic loss of diapause.

#### 128 Dispersion

129 Poethke et al. (2010) [28] showed with a model that any persistent deterioration of the environment that decreases  
130 expected fitness can induce dispersal behaviour in philopatric organisms. The model was developed for aphids  
131 responding to declining population viability due to increased predation pressure, but the model can be applied to any  
132 environment deterioration that reduces population viability.

#### 133 Interspecific interactions

134 Interactions between species depend on local conditions and, hence, are sensitive to environmental change [29, 30].  
 135 Pesticides, for instance, shift the competitive relationship between two thrips species so that an intrinsically inferior  
 136 species *Frankliniella occidentalis* displaces an intrinsically superior competitor *Thrips tabaci* [31]. Climate change and  
 137 increases in temperature are similarly altering species interactions. Ground beetles, for instance, attack more mobile  
 138 prey at higher temperatures [32], while the parasitoid *Aphidius rhopalosiphi* attack fewer aphid hosts [33].  
 139 The invasion of alien species can profoundly alter species interactions and thereby the dynamics of populations [34].  
 140 When the mosquito *Aedes albopictus* - a vector of Zika, dengue, and chikungunya viruses - invaded North America, it  
 141 displaced the resident *Ae. aegypti* through interspecific matings that sterilized the resident species [35]. However,  
 142 invaders can as well have positive effects on ecosystems. When insect pollinators were introduced to the Galapagos  
 143 Islands, these made more visits to plants than the native species, which improved the stability of the interaction network  
 144 [36].  
 145 The loss of species can similarly alter species interactions. When large herbivores were lost from the African savanna,  
 146 *Acacia* trees invested less in food and shelter rewards for mutualistic ants, which defend the trees against large  
 147 herbivores and insect pests. A non-mutualistic ant could then occupy the trees, which caused the trees to suffer  
 148 increased attack by insect pests [37].  
 149 Social behaviour  
 150 Social behaviour is an important determinant of fitness in social insects. Thus, alteration of social behaviour because of  
 151 environmental change can have profound demographic consequences [38, 39]. For instance, higher temperature  
 152 induces a switch from solitary to social lifestyle in sweet bees *Halictus rubicundus*, which increases the number of  
 153 pollinators, which in turn could mitigate the current pollinator crisis [40]. On the other hand, a rise in temperature can  
 154 as well disrupt social interactions. For example, higher temperature increases variation in worker size in the ant  
 155 *Temnothorax nylanderi*, probably through reduced ability of nestmate workers to regulate larval development [41].  
 156 Changes in the distribution and abundance of resources are common causes of altered frequency or type of social  
 157 interaction. Changed shelter availability, for instance, influences the formation of social aggregations in the maritime  
 158 earwig *Anisolabis maritima* [42]. In the pharaoh's ant *Monomorium pharaonic*, changed resource distribution influences  
 159 pheromone deposition along trails to food sources, which allows ants to communicate and reach adaptive collective  
 160 decision in changing environments [43].  
 161 Is behavioural plasticity sufficient to cope with human perturbation?

162 In this review, we have shown that behaviourally plastic response to HIREC are common. However, whether the plastic  
163 responses are sufficient to prevent population decline and extinction is poorly known. The research field is still in its  
164 infancy, and examples are scarce for insects. Some species are able to adjust their behaviour in an adaptive manner to  
165 changes, such as bark beetles that use multiple, integrated sensory modalities to adjust their choice of host trees to  
166 local conditions [9]. However, an increasing number of studies find species to respond maladaptively or insufficiently to  
167 various anthropogenic disturbances. For instance, plasticity in feeding behaviour of the harvester ant *Pogonomyrmex*  
168 *mendozanus* is insufficient for coping with deteriorating food quality [9]. Similarly, most species have limited potential  
169 to adjust behaviourally to extreme temperatures and many species are moving towards the poles to escape climate  
170 change [25, 44].

171 Ecological traps can worsen survival prospects in changing environments. For instance, jewel beetles (*Julodimorpha*  
172 *bakewellii*) copulate with beer bottles because the texture of the bottles resembles that of females [45], while mayflies  
173 oviposit on asphalt because the surface reflects polarized light in a similar manner as water bodies [46].

174 Behavioural responses that are insufficient but still improve survival could facilitate evolutionary adaptation by  
175 providing more time for genetic changes [47]. This is especially likely in species with short generation time, as suggested  
176 for many pest and disease vectors [48].

## 177 Conclusions and perspectives

178 Behavioural plasticity is often not sufficient to cope with HIREC. One explanation is proposed by Sih (2013) [5]: if novel  
179 items have been poor options in the evolutionary history of a species, this could explain neophobic behaviours, while if  
180 novel items have been beneficial in the past, this could explain neophilic behaviours, which can help species to respond  
181 to HIREC. Because HIREC often results in novel conditions, not experienced in the recent evolutionary past, the  
182 responses may often be maladaptive and result in population decline. In rare cases, human induced changes can have  
183 a positive effect on an ecosystem's stability. For instance, in the Galapagos Islands, an introduced pollinators visited  
184 more plants than their native or endemics counterparts, which increased ecosystem stability [36, 49].

185 Two fields of research emerge from this review that need more attention: (1) from a fundamental point of view, more  
186 research is needed on the effects of transgenerational plasticity on behavioural responses to environmental change, ie,  
187 when environments experienced by the parents influence the responses of offspring. Transgenerational plasticity is  
188 increasingly found to be involved in adjustments to variable environments, but the degree to which insects adjust to  
189 HIREC through transgenerational plasticity in behaviour is a largely unexplored topic. (2) From an applied point of view,



190 the field of Conservation Behavior should receive more attention. This is a young discipline that investigates how the  
191 knowledge of animal behaviour can be taken in consideration in actions for preventing the loss of biodiversity [50].

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Figure legend

Figure 1 (adapted from Sih 2013 [5]). Extended reaction norms. Within a range of normal past conditions, animals might show optimal reaction norms that match environmental optima reasonably well. In condition A, just outside of the range of past conditions, organisms might simply extend their reaction norms; however, beyond some threshold (condition B), lack of past selection might allow the maintenance of genetic variation in reaction norms, some of which might come close to matching even a very different optimum in a novel condition that is well outside the range of past conditions. The stars represent the optimal trait in each environment.

